In a long-term experimental demography study, excluding ungulates reversed invader’s explosive population growth rate and restored natives

Susan Kalisz\textsuperscript{a,1}, Rachel B. Spigler\textsuperscript{a,2}, and Carol C. Horvitz\textsuperscript{b}

\textsuperscript{a}Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260; and \textsuperscript{b}Department of Biology, University of Miami, Coral Gables, FL 33124

A major goal in ecology is to understand mechanisms that increase invasion success of exotic species. A recent hypothesis implicates altered species interactions resulting from ungulate herbivore overabundance as a key cause of exotic plant domination. To test this hypothesis, we maintained an experimental demography deer exclusion study for 6 y in a forest where the native ungulate \textit{Odocoileus virginianus} (white-tailed deer) is overabundant and \textit{Alliaria petiolata} (garlic mustard) is aggressively invading. Because population growth is multiplicative across time, we introduce metrics that correctly integrate experimental effects across treatment years, the cumulative population growth rate, $\lambda$, and its geometric mean, $\lambda_{\text{per-year}}$, the time-averaged annual population growth rate. We determined $\lambda$ and $\lambda_{\text{per-year}}$ of the invader and of a common native, \textit{Trillium erectum}. Our results conclusively demonstrate that deer are required for the success of \textit{Alliaria}; its projected population trajectory shifted from explosive growth in the presence of deer ($\lambda_{\text{per-year}} = 1.33$) to decline toward extinction where deer are excluded ($\lambda_{\text{per-year}} = 0.88$). In contrast, \textit{Trillium’s $\lambda_{\text{per-year}}$ was suppressed in the presence of deer relative to deer exclusion ($\lambda_{\text{per-year}} = 1.04$ vs. 1.20, respectively). Retrospective sensitivity analyses revealed that the largest negative effect of deer exclusion on \textit{Alliaria} came from rosette transitions, whereas the largest positive effect on \textit{Trillium} came from reproductive transitions. Deer exclusion lowered \textit{Alliaria} density while increasing \textit{Trillium} density. Our results provide definitive experimental support that interactions with overabundant ungulates enhance demographic success of invaders and depress natives’ success, with broad implications for biodiversity and ecosystem function worldwide.

\begin{itemize}
  \item life table response experiment
  \item herbivory
  \item biotic resistance
  \item temperate deciduous forest conservation
  \item forest understory herbs
\end{itemize}

Safety increasing pressure by invasive plant species on native biodiversity (1) disrupts both community and ecosystem function (2) and results in staggering economic costs worldwide (3, 4). A major goal in ecology is to understand how changes over time in species interactions affect invasion success of exotic species (5–8). According to ecological theory, the ability of the resident community to limit the success of invading exotics [biotic resistance (9, 10)] will depend upon ecological context that includes the suite of local interactors (11–15). The abundance of herbivores and their local impacts (11, 14, 16) can play a prominent role in how fast plant populations grow or shrink and how much the relative abundance of plant species changes over time (5, 15), including changes associated with plant invasions (11, 16–19). Recently, increased browsing pressure by overabundant ungulate herbivores on native plant communities has been proposed as a fundamental cause of a shift from native to exotic plant domination in forests and rangelands worldwide (11, 16, 20). Wild and domesticated ungulates (e.g., deer, elk, goats, sheep, horses, cows) that are either native or introduced have all been implicated in this process (11, 16, 20).

Overabundant ungulates may change the success of invading exotics in numerous ways. Ungulate browsing on natives may depress their abundance and ability to compete (21–24) and increase abiotic resources available to invaders (11, 25, 26), which can act synergistically to decrease communities’ ability to resist invasion (biotic resistance; refs. 8 and 10). Ungulates disperse exotic seeds (27, 28) and create novel abiotic conditions with respect to soil disturbance, soil quality, and light availability (21, 22, 26), which may enhance exotic establishment and growth. Moreover, although ungulates are considered diet generalists, in fact, they frequently behave as selective foragers (21–24, 29), preferring natives to exotics. In this circumstance, unpalatable invaders can have a double advantage over natives—both release from historic enemies (20) and inedible to new potential enemies in the invaded range (30, 31). Together, these mechanisms not only implicate overabundant ungulates in their direct impact on the rate at which populations of palatable native species grow or shrink, but point to their potentially pivotal role in reducing the biotic resistance of the native community to favor invaders (13, 14).

To determine how ungulate herbivores affect the fitness of invaders and natives, field experiments that manipulate herbivore access for several years and are spatially well replicated are required (11, 32, 33). The multiyear, population-level demographic data gained in such experiments can be used to estimate the ultimate metric of fitness: population growth rate ($\lambda$). However, despite the widespread use of manipulative experiments that alter herbivore access to plants, we still lack appropriate demographic data (i.e., complete schedules of fertility, mortality and growth

Significance

In ecosystems worldwide, the presence of overabundant ungulates (e.g., deer, cows) and the invasion of exotic plants are disrupting native communities. A recent hypothesis causally links these problems implicating overabundant ungulates in enhancing invaders’ demographic success. We tested this hypothesis in a forest where white-tailed deer are overabundant and garlic mustard is aggressively invading. Using long-term, replicated deer exclusion/deer access plot pairs, we quantified population density, growth, and decline of this invader and native plants. We conclusively demonstrate that deer are required for garlic mustard success; its local extinction is projected where deer are absent. Our findings provide the first definitive support connecting overabundant ungulates to enhanced invader success, with broad implications for biodiversity and ecosystem function.

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To whom correspondence should be addressed. E-mail: kalisz@pitt.edu.

Present address: Department of Biology, Temple University, Philadelphia, PA 19122.

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estimates the total leaf area of a species, often relative to
Alliaria  
Trillium  
14-m plots) with one plot per pair
=  
Kalisz et al.  
Alliaria  ranks among the
as it is the most common flowering
01.40  
represents a model for under-
www.pnas.org/cgi/doi/10.1073/pnas.1310121111
as
and one of
Alliaria  reveal how each part of the life cycle contributes to overall
Alliaria  –
was lower and that there was signifi-
"|
Trillium  has a rapid, biennial life cycle: spring seedlings form
fitness would in-
and 43), our study is distinct. We know of no other such
conduct a definitive demographic experiment that could distin-
unified answer regarding exotic invaders [effect on invasion
(S1 2004 revealed overabundant deer: currently 20–42 deer per km²
compared with an historic density of 10–12 deer per km² (Fig. 51). In a different area in this same forest, Knight et al. (39) used an indirect metric of plant performance and found that relative
table of population vi-
viability of invaders or natives. Also, although evidence of ungulates’
influence on native plant population dynamics from exclusion
experiments has been previously demonstrated (e.g., refs. 42
and 43), our study is distinct. We know of no other such
experiments testing the link between ungulates and invasive
exotic population growth rate in invaded systems.
Here, we use experimental demography and stage-based data
(rates of survival, fertility, and growth) collected over multiple
years in high-elevation forests that are in marked contrast to
herbivore drives positive population growth of invaders (11, 16).
We emphasize that in herbivore removal experiments the fitness
of plant populations, which is measured by population growth rate, is predicted to rebound with persistent, multiplicative
beneficial effects over time. What has not previously been rec-
noculated in such experiments is that treatment effects accumulate
over the span of an experiment (44), necessitating a quantitative
metric that integrates fitness over the entire life cycle and over
time. Moreover, population growth is a process that is multipli-
cative across time. Thus, we introduce the use of cumulative
population growth rate, λ, at the end of a multiyear
experiment as the metric that correctly integrates experimental effects across
the observed sequence of demographic changes across time. Our
multiyear demographic projection and the corresponding mul-
tiyear retrospective sensitivity analysis provide fresh insights.
To facilitate comparisons of our results with studies that estimate λ
from single-year transitions, we present λper-year, the geometric
mean of λ. Our retrospective sensitivity analyses [similar to life
table response experiment analysis for periodic matrices (45, 46)]
of λ reveal how each part of the life cycle contributes to overall
differences in population growth caused by experimental
manipulation. We conclusively show that over-
abundant deer create conditions favorable for explosive ex-
ponential population growth of an exotic plant invader, but
that when deer are excluded, populations of the invader are
projected to decline exponentially.
We focus on the native ungulate Odocoileus virginianus (white-
tailed deer; hereafter, deer) and the exotic herbaceous under-
dstory invader Alliaria petiolata (Brassicaceae; garlic mustard; hereafter, Alliaria), which both present serious management
concerns in North American forests. Relative to historical records,
derer densities are currently 4–10 times higher than pre-Euro-
pean settlement densities across North America (47). Over-
abundant native deer in forests exert the same kinds of pressures
as other ungulates (native and nonnative, wild and domesti-
cated) globally, including perturbation of understory com-
unities (22, 27, 39), exotic seed dispersal (27), and alteration of
abiotic conditions (21, 39). Likewise, Alliaria ranks among the
most problematic forest invaders in North America (48). In-
trouded by early colonists, it was naturalized on Long Island,
New York, by 1868 (reviewed in ref. 48). In its native Eurasia, Alliaria grows in edge or disturbed habitats, whereas in North
America it increasingly occupies forest interiors (48). Relative to
the slow-growing, long-lived understory community it invades, Alliaria has a rapid, biennial life cycle: spring seedlings form
overwintering rosettes by autumn. In their second year, plants
reproduce, disperse seeds, and die. In its invaded range, Alliaria has high population growth rates (λ = 1.4–3.4) (48), which pro-
ject annual increases in numbers of 40–240%. Alliaria’s
invasive success has been hypothesized to result from various
factors. These include the following: novel allelopathic weapons,
enemy release, positive soil feedback, taxonomic novelty, high
competitive ability, and specific phenotypic traits. No single
factor has yet to explain the broad reach of this tenacious exotic
(reviewed in ref. 48). Here, we investigate what has not been
previously explored: the role of ungulate disruption of native
community biotic resistance (13) on Alliaria’s invasion success.
To date, deer and Alliaria have been focl of intense, largely
separate, research efforts. Our approach uses experimental de-
mography to jointly examine these two issues. Together, they
constitute an ideal system to investigate ungulate–exotic plant
invasion linkages (11, 16).
Our experiment was conducted in a beech–maple forest in
southwestern Pennsylvania (Trillium Trail Nature Reserve,
Allegheny County, Pennsylvania: 40° 52’ 01.40” N; 79° 90’ 10.75” W), Winter aerial flyovers of this area performed between 1993–
2004 revealed overabundant deer: currently 20–42 deer per km²
just after an indirect metric of plant performance and found that relative
differences in cumulative population dynamics caused by an
invader
constitute an ideal system to investigate ungulate–exotic plant
invasion linkages (11, 16).
Alliaria’s population growth rate to remain high despite deer exclusion, while predictions for the effects of deer on the natives remain the same. In brief, from 2003 to 2008 at annual censuses, we scored reproduction and survival of individuals of Alliaria and of the three native perennials that are preferred food sources for deer (49): Trillium, Maianthemum racemosum (Rutaceae), and Polygonatum biflorum (Rutaceae). In plots accessible to deer, we also scored deer browse. To assess the effect of deer exclusion on the fitness of Trillium and Alliaria, we implemented our multiyear matrix projection analysis to calculate cumulative population growth rates from 2003 to 2007 for each treatment. To construct matrices, we defined five life cycle stages for the perennial Trillium (germinant bank, seedling, one-leafed juvenile, three-leafed nonflowering, and three-leafed flowering: Fig. S2A) and three life cycle stages for Alliaria (dormant seed in the seed bank, rosette, and fruiting adult: Fig. S3A). Matrix elements were calculated as a function of the vital rates associated with each stage transition (Figs. S2A and S3A). We captured cumulative effects of deer exclusion or continued deer overabundance over time, parameterizing multiyear projection matrix models B, for each species and treatment by multiplication of annual projection matrices $A_{\text{YEAR-TREATMENT}}$ (e.g., $B_{\text{DEER}} = A_{0005-\text{DEER}} A_{0005-\text{DEER}} A_{0004-\text{DEER}} A_{0003-\text{DEER}}$). The matrix $B$, at the heart of our analyses, contains the rates at which individuals that were at a given stage at the beginning of the experiment will have either become or produced individuals of each stage after four transition years. Our analyses of multiyear matrices provide integrative measures of plant fitness over the time frame of the experiment, including treatment-specific cumulative population growth rates ($\lambda$, the dominant eigenvalue of $B$), time-averaged $\lambda$’s ($\lambda_{\text{per-year-TREATMENT}}$ = the fourth root of the dominant eigenvalue, $\lambda$, of $B$), and an overall measure of the effect of protecting plants from deer on plant fitness $\Delta \lambda_{\text{per-year}} = \lambda_{\text{NO-DEER}} - \lambda_{\text{DEER}}$. [Note: Pooled plot data (Trillium) and individual plot data (Alliaria) were used. See Materials and Methods, Matrix Construction For Each Species and Treatment.] Finally, to uncover mechanistic differences between the response of the native and the exotic to deer exclusion, we use a life table response experiment retrospective sensitivity analysis (45, 46). The analysis shows how important each of these 4-y demographic rates is to differences in $\lambda$ between treatments, quantified by contributions made during transitions from stage $j$ to stage $i$, $c_{ij}$.

Results
Over the course of the experiment, 2003–2008, we collected data on >9,000 individually tagged plants in six paired plots. In plots where deer had access, they browsed an average of 22% (±0.08 SD) of the palatable native individuals per year ($n = 6$ y), with dramatic consequences for reproduction of all three species (Fig. 1). At the start of the experiment, only 2–3% of the natives were reproductive in either treatment, but beginning in 2004, the percentage of native individuals that reproduced in the plots protected from deer increased dramatically (Fig. 1B). In contrast, this percentage remained low where deer had continual access. By 2008, 26% of natives in plots protected from deer successfully reproduced compared with only 5% where deer had continuous access (G statistic = 254.7, $P < 0.0001$). These results demonstrate large negative effects of deer on the reproductive capacity of the natives.

The restoration of reproduction in plots where deer were excluded translated into significant increases in the population-level fitness of the native Trillium. In the plots protected from deer, the Trillium population is projected to increase 20% annually ($\lambda = 1.20; 95\%$ confidence interval (CI): 1.18–1.22; $n = 5,000$ bootstrap samples). In the plots where deer were allowed access, population growth was substantially lower ($\lambda = 1.04; 95\%$ CI: 1.03–1.06; $n = 5,000$ bootstrap samples). A permutation test comparing the two treatments $\lambda_{\text{per-year}}$ revealed that the overall improvement in Trillium’s fitness due to its protection from deer, $\Delta \lambda_{\text{per-year}} = 0.16$, is significant ($P = 0.0002; n = 5,000$ permutations). Our retrospective sensitivity analysis (45) clearly shows that differences between treatments in the demographic rates of the flowering stage made the greatest contribution to the differences in population growth rate between the treatments (Fig. 24). Protection from deer over the course of the experiment resulted in flowering plants with a higher probability of remaining reproductive and a lower probability of becoming nonflowering over this period. Similarly, nonflowering plants had a higher probability of becoming reproductive and a lower probability of remaining nonproductive (Fig. 24). These effects combine to generate significantly higher population growth where deer were excluded. The effect of deer on Trillium’s projected population growth mirrors the change in actual Trillium abundance seen across the study period in the two treatments (Fig. 3).

In contrast, deer never browsed Alliaria in our experimental plots. In fact, the presence of deer ensures Alliaria’s high population growth rate and high density. At the start of our experiment, Alliaria was increasing in both treatments, and its fitness did not differ significantly between the treatments: $\lambda_{0003-\text{DEER}} = 1.11$ (SEM = 0.07) vs. $\lambda_{0003-\text{NO-DEER}} = 1.28$ (SEM = 0.14) (Fig. 44). However, Alliaria’s population growth rate diverged dramatically between treatments by the end of the experiment. Where deer had continuous access, fitness over the duration of the experiment remained high and not significantly different from the start of the experiment ($\lambda_{\text{per-year-DEER}} = 1.33$, SEM = 0.11; Fig. 44). Conversely, in the plots protected from deer, fitness declined by ~40% relative to the start of the experiment ($\lambda_{\text{per-year-NO-DEER}} = 0.88$, SEM = 0.09; Fig. 44) and was significantly less than 1.0. Thus, we found a large, negative fitness difference due to long-term protection from deer, $\Delta \lambda_{\text{per-year}} = -0.45$. Overall, where deer are present, Alliaria populations are
increasing ~30% annually, but in plots protected from deer they are declining ~12% annually and if conditions remain the same, all will eventually go extinct, according to model projections. The initial spatially weighted mean population density in the deer exclusion plots was 8.9 adults per m². Our projection indicates the extinction threshold (defined conservatively as a density of 0.005 adults per m², <1 individual within each 14 × 14-m plot) would be reached after 58.6-y. Our annual field censuses corroborate the projected decline. Over the course of the experiment, Alliaria adult density in plots protected from deer declined 58% but did not decline in plots where deer had access (Fig. 4B). Our retrospective sensitivity analysis shows that the rate at which rosettes at the beginning of the experiment have produced rosettes after 4 y is the most important of these 4-y demographic rates for Alliaria (Fig. 2B). We emphasize that many processes (survival, growth, and reproduction) across seasons and across years are multiplicative components of this 4-y rosette-to-rosette rate. All aspects of the invaders’ life cycle are stifled where plants are protected from deer, because every matrix element made negative contributions to the difference in λ between treatments (Fig. 2B). This result is in stark contrast to the positive effects of the contributions in Trillium when plants are protected from deer (Fig. 2B).

Discussion

Our results conclusively link Alliaria’s invasion success to the presence of an overabundant native ungulate, white-tailed deer. Alliaria’s population growth rate remained explosive where deer had continual access throughout the experiment, but without deer, Alliaria is projected to decline to extinction. Our results on the recovery of native species highlight the potential role of biotic resistance and deer-mediated shifts in invader–native community interactions. Upon release from intense deer pressure in the deer exclusion treatment, the three native species exhibited positive fitness responses as measured by their increased reproductive success (Fig. 1B). Consequently, Trillium exhibited increased seedling recruitment (Fig. 3) and a higher population growth rate where deer were excluded; λ_{year} increased from 1.04 with deer to 1.20 in their absence. Indeed, the fittestnesses of the native species and Alliaria are reversed by changes in the abiotic and biotic contexts in our treatments (Fig. 2A vs. B). In addition to suppressing native species as shown here, a companion experiment at our study site (39) demonstrated that deer negatively affect the abiotic context, which could favor short-lived species like Alliaria (48). In that study, the area with deer present had significantly more bare ground relative to the area where deer were excluded (39). These openings are likely the combined results of soil disturbances by deer and leaf removal from palatable species in the understory by deer browse, which could increase light levels at the soil surface. Our results point to the restoration of the potent biotic resistance of the native community to Alliaria through management of overabundant deer.

Our results also shed light on multiple additional hypotheses for Alliaria’s invasion success. Because Alliaria cannot flourish in this forest without deer, our results suggest that previous hypotheses for Alliaria’s invasion success (48) may be context dependent. In contrast to studies that demonstrate how native herbivores can increase biotic resistance by consuming invaders (18), our findings show that deer, a native generalist ungulate, find the invasive Alliaria completely inedible, which undoubtedly bolstered its fitness where deer had access (39, 41). Thus, our data lend support to the hypothesis that a lack of palatability may be a general trait of highly successful invaders (16, 53), particularly in communities with overabundant ungulates (54, 55). Although we did not directly test other hypothesized mechanisms of invasion attributed to widespread exotics Including Alliaria (i.e., enemy release from specialist herbivores, novel weapons and allelopathy, positive soil feedbacks, competitive ability) (reviewed in ref. 48), our results indicate that either individually or in combination, these mechanisms were not sufficient to maintain Alliaria’s population proliferation when...
deer were excluded. However, these factors may act to further enhance this invader’s success in the context of abundant deer.

In forest and rangeland ecosystems across the globe, the domination of native plant communities by exotic species and declines in biodiversity are becoming widespread crises (1, 4, 16). Co-incidently, recent changes in management of land, livestock, game, and wildlife have resulted in unprecedented increases in managed (e.g., cattle, goats) and wild native (e.g., deer, moose, elk) ungulate pressure and ungulate abundance (22, 47, 56) and are likely more susceptible to invasion than those with a long history of browsing (57). If the results of our experiment apply generally, then reducing ungulate numbers where they are over-abundant will be key in curbing invasion success in forest and rangelands worldwide. These habitats are in particular need of policy and management practice reform, because their ecosystem functions are predicted to further decline over time as community diversity degenerates (58) and functional redundancy is lost (59).

Finally, our findings underscore the need for management strategies for ungulates and invasive plants to maintain functional native–invasive interactions that preserve biodiversity.

Materials and Methods

Field Logistics for All Species. Paired plot locations were chosen in Spring 2002 spanning the range of habitats in this forest where our focal species were found to co-occur. In Fall 2002, we established paired plots (n = 6 pairs of 14 x 14-m plots). One plot per pair was randomly assigned to a fenced treatment that excluded deer, eliminating only deer without allowing all other animals (e.g., turkeys, passerines, rabbits, squirrels, chipmunks, rodents) free access. Fenced plots were enclosed with 3-m-high, 15 x 15-cm steel mesh fences. Fences were maintained continuously, creating two treatments: deer access and deer exclusion. Each plot contained 36, 4-m² subplots, with footpaths every 4 m to ensure minimal disturbance by data collectors. To assess the abundance and the reproductive and browse statuses of Trillium erectum (Melanthiaceae), Maianthemum racemosum (Ruscaceae), Polygonatum biflorum (Ruscaceae), and Alliaria petiolata (Brassicaceae) individuals, we determined flowering in early spring, deer browse at time of each species’ bloom, and fruiting success in midsummer every year through 2008. Fruiting of the three native species was not assessed in 2003 and 2004; therefore, to approximate the percentage of plants that successfully reproduced (Fig. 1), we assumed that flowering plants that were not eaten or damaged set fruit; otherwise, they did not. Reproduction of natives across treatments and years was compared using G tests. The bite angle of deer is distinct from other mammals, and deer-browsed stems were readily identified.

Matrix Construction for Each Species and Treatment. In our plots, we assessed annual densities (plants per square meter) and measured stage-specific survival and reproduction of the focal species. To calculate the vital rates needed for annual projection matrix construction for Trillium erectum and Alliaria petiolata, we followed the fates of tagged individuals annually. Details of the field methods and vital rate calculation for each species are presented in SI Text. Using the vital rates for Trillium (Fig. S2A) and Alliaria (Fig. S3A), we constructed annual population projection matrices, A_{YEAR,TREATMENT}, with elements a_{ij} for Trillium (Fig. S2B) and Alliaria (Fig. S3B).

For Trillium, which varied in abundance among the pairs of plots (and was absent from the habitat represented by one of the pairs), we created a single matrix for each treatment and transition year, pooling data across all plots of a given treatment (fenced vs. unfenced, abbreviated NO.DEEER and DEER) for each of the transition years (2003–2004, 2004–2005, 2005–2006, 2006–2007, abbreviated 2003, 2004, 2005, and 2006). This resulted in a site-wide spatial average, where the weighting for Trillium was by abundance of individuals in each plot.

For Alliaria, which was abundant in all plots, we created separate annual matrices for each plot, six matrices for fenced plots (not accessible to deer) and six matrices for unfenced plots (accessible to deer), for each of the four transition years. Within the range of areas where our focal species were present in Trillium Trail, we chose plots to span the gradient in topography from level to sloped, locating matched pairs along this gradient. We then determined the proportion of the total area of Trillium Trail that was similar to each matched pair. Thus, we were able to apply a weighted average to the data that was representative of the habitats where our focal species were found at the study site. Each plot pair (1-6) was weighted 10%, 10%, 20%, 20%, 20%, and 20%, respectively. To scale up to the level of the entire study site, we created a spatial average by weighting our single plot results accordingly. This resulted in a site-wide spatial average for each transition year and treatment, where the weighting for Alliaria was by abundance of the habitat at the site.

For Trillium, the transition year 2003–2004 was not considered to measure a pretreatment, baseline removal of this species (and indirectly browse this species) has immediate effects on demographic rates. For Alliaria, the transition year 2003–2004 was considered to measure a pre-treatment, baseline condition, because removal of deer (who alter soil and eat palatable native species) is expected to have a delayed effect on demographic rates. Thus, as a measure of expected population dynamics if deer were maintained at ambient levels, we report the spatially averaged asymptotic population growth rates from the A_{2003-NO_DEEER} and A_{2003-DEER} matrices for this species and across all pairs of plots, and report the SEs among the plots scaled by the spatial weightings.

In addressing the effects of 4 y of deer exclusion on population dynamics of natives and exotics, we note that population dynamics are multiplicative and effects of deer exclusion are cumulative over time. Thus, we determined multyear projection matrices B for each species and treatment.

For Trillium (where we had a single annual projection matrix for each year), B_{NO_DEEER} = A_{2003-NO_DEEER} A_{2004-NO_DEEER} A_{2005-NO_DEEER} A_{2006-NO_DEEER} A_{2007-NO_DEEER} and B_{DEER} = A_{2003-DEER} A_{2004-DEER} A_{2005-DEER} A_{2006-DEER} A_{2007-DEER}. We calculated the cumulative population growth rate over a 4 y time step, λ, (the dominant eigenvalue of each B) and its fourth root, λ_{pop-year}, Which measures the time-averaged annual growth rate over the experimental time frame. We constructed 95% bootstrap CIs for each λ_{pop-year} to evaluate whether significantly different from 1 (no growth) [n = 5,000 bootstraps (47)]. We used a permutation (randomization) test to evaluate whether λ_{pop-year} differed significantly between treatments [n = 5,000 permutations (47)]. For Alliaria, we determined B for each plot across 4 y and found its dominant eigenvalue and its time-averaged annual growth rate. Then applying the habitat weightings, we calculated a spatially weighted average λ_{pop-year} for each treatment at our site. For this species, our replicates were the plots, and we report the SEs among the plots scaled by the spatial weightings.

Multyear Cumulative Growth Retrospective Analysis. To uncover mechanistic differences between the response of the native and the exotic to deer exclusion, we used a life table response experiment analysis (47), which decomposes treatment-level differences in plant fitness into contributions from each matrix element.

Fig. 4. (A) Per year population growth rate (± SEM) of the exotic Alliaria petiolata in deer access and deer exclusion plots at the start of the experiment (Start, single transition year 2003–2004) and after 5 y of treatment (λ_{pop-year} = time averaged annual growth rate, the fourth root of the 4 y cumulative growth rate). Alliaria’s z declined significantly where deer were excluded, but remained high in deer access plots. (B) Deviation of Alliaria adult density (adults per square meter ± SEM) from initial adult density in deer access plots (blue diamonds) and deer exclusion plots (blue squares) 2004–2008. Adult density ranged from 1 to 16 adults per m² (mean = 5.4) in deer access plots and from 2 to 17 adults per m² (mean = 9.4) in deer exclusion plots. Alliaria is a biennial species in which adult plants predominate in alternate years with the rosette-stage plants. Thus, adult densities are shown in 2004, 2006, and 2008 only. Alliaria adult densities declined significantly in deer exclusion plots with no change in deer access plots.
For *Trillium*, there was one 4× matrix for each treatment $B_{DEER}$ and $B_{NO\ DEER}$. We defined a reference matrix as the mean across-treatment matrix, used to calculate the sensitivity $s_{ij}$ of $j_i$ to each matrix element. The difference in matrix elements between treatments is $\Delta b_{ij} = B_{NO\ DEER} - B_{DEER}$. The product $(s_{ij} \cdot \Delta b_{ij})$ for each element provides its contribution, $c_{ij}$, to the difference due to the exclusion of deer.

For *Allaria*, we constructed matrices whose elements were obtained by starting with the 4-y matrices of each plot, $B_j$. Matrix elements were averaged across plots, weighing each as above for spatial representation of each pair across the study site, to obtain a single mean $(\mathbf{B})$ and its corresponding $s_{ij}$ for each experimental treatment. We defined a reference matrix as the mean across-treatment matrix, used to calculate the sensitivity $s_{ij}$ of $j_i$ to each matrix element. The difference in matrix elements between treatments is $\Delta b_{ij} = B_{NO\ DEER} - B_{DEER}$. The product $(s_{ij} \cdot \Delta b_{ij})$ for each element provides its contribution, $c_{ij}$, to the difference due to the exclusion of deer.

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